Parentally biased favouritism: why should parents specialize in caring for different offspring?

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'Parentally biased favouritism' occurs when the two parents differentially care for individual offspring or kinds of offspring. Examples in birds include brood division and differential investment by the two parents in relation to the size or sex of the offspring. This paper uses mathematical models to investigate which ideas can, in theory, explain parentally biased favouritism. One previous explanation is that the parents differ in their cost of reproduction and that the parent who consequently invests least concentrates its care on the more valuable offspring. However, a mathematical model predicts the total care given by each parent and received by each offspring, not how much each parent cares for each offspring, and hence does not explain parentally biased favouritism. Parentally biased favouritism towards particular types of offspring can be explained by a difference between the parents in the benefits of caring for a given type of offspring or in the effort incurred in providing care to a given type of offspring, but then it is extreme, with at least one of the parents providing care to only one type of offspring. Parentally biased favouritism towards particular individual offspring (brood division) can be explained by parent-offspring conflict or sexual conflict.

Keywords: parental favouritism; parental investment; parental care; parent-offspring conflict; sibling competition; sexual conflict

1. INTRODUCTION

In species with biparental care and families of more than one offspring, there are essentially three kinds of departure from a uniform provision of care by the two parents to different offspring (Stamps *et al.* 1987; Lessells 1998). First, the amount of care provided may differ between the two parents. Second, different offspring may receive different amounts of care. Sometimes such favouritism can be related to variation between the young in characters such as sex, size or age. In other cases, differences in parental care may be unrelated to any pre-existing differences, for example, when there is variation in the maternal provisioning of eggs or embryos. These first two kinds of bias can co-occur independently, but there may also be an interaction between them. It is this third kind of bias—parentally biased favouritism—in which the two parents care differentially for individual offspring or kinds of offspring, that I consider.

Under some circumstances, the evolution of parentally biased favouritism is fairly readily understood: when more than one form of care is provided by the parents, morphological, physiological or behavioural specialization of the male and female will often select for a division of labour in which the two parents provide different components of care, such as defence, shelter or provisioning. If the offspring also differ in their need for these kinds of care, parents should care differentially for these young.

Parentally biased favouritism is harder to understand when care appears to be provided in only one form, as is the case for many bird species provisioning their young. Some of these examples may conceal instances where there are differences in the kind of care provided. For instance, in budgerigars *Melopsittacus undulatus*, the parents regurgitate food for the chicks. The extent to which the food is pre-processed by the parent varies with the age of the chick (A. B. Clark, personal communication), so the two parents might be expected to specialize in feeding different age chicks within the brood. (Hatching asynchrony is considerable in this species.) This might provide an explanation as to why male budgerigars feed in response to begging, while females ignore begging and seek out, and preferentially feed, the smallest chicks (Stamps *et al.* 1985). However, cryptic differences in the kinds of care provided by the two parents are unlikely to be common, and in many of the examples given there is no reason to suppose that such differences exist. At least four different manifestations of parentally biased favouritism in chick provisioning are known:

- (i) *The two parents feed different-sized young differentially.* Some variation in the size of young within a brood is always to be expected, but it is commonly increased by hatching asynchrony, where differences in the size of young reflect variation in hatching date within a brood (Magrath 1990). A number of studies have shown that male and female parents do not provision young of different sizes equally, with female parents often feeding the smaller young

Table 1. A review of parentally biased favouritism in relation to chick size in birds (after Slagsvold 1997a). The letters in the body of the table indicate the sex of the parent preferentially feeding the smaller chick(s) in the brood: M/m, male; F/f, female; —, no interaction between parental sex and chick size. An upper-case letter indicates statistical significance at $p < 0.05$ using the brood as the unit in the analysis. A lower-case letter indicates that $p < 0.1$ using the brood as the unit of analysis, individual chicks were used as the unit in the analysis, or the interaction between parental sex and chick size was not tested. In the references, C means captive study and E means experimental study.

species	sex of parent preferentially feeding smaller chick(s)			reference
	nestling period	partially fledged	post-nestling period	
white ibis (<i>Eudocimus albus</i>)			—	Frederick (1987)
black coot (<i>Fulica atra</i>)			f	Horsfall (1984)
common snipe (<i>Gallinago gallinago</i>)			F	Tuck (1972)
budgerigar (<i>Melopsittacus undulatus</i>)	F			Stamps <i>et al.</i> (1985) (C)
crimson rosella (<i>Platyercus elegans</i>)	F			Krebs <i>et al.</i> (1999)
flamulated owl (<i>Otus flammeolus</i>)			—	Linkhart & Reynolds (1987)
pallid swift (<i>Apus pallidus</i>)	—			Malacarne <i>et al.</i> (1994)
Eurasian swift (<i>Apus apus</i>)	—			Martins & Wright (personal communication in Slagsvold (1997a))
tree swallow (<i>Tachycineta bicolor</i>)	F			Leonard & Horn (1996)
dunnoch (<i>Prunella modularis</i>)			—	Byle (1990)
European robin (<i>Erithacus rubecula</i>)		f	M	Harper (1985)
bluethroat (<i>Luscinia svecica</i>)			—	Anthonisen <i>et al.</i> (1997)
	—			Smiseth <i>et al.</i> (1998) (E)
blackbird (<i>Turdus merula</i>)		f		Bengtsson & Rydén (1981)
American robin (<i>Turdus migratorius</i>)	—		—	Weatherhead & McRae (1990)
	—	f		Slagsvold (1997b)
pied flycatcher (<i>Ficedula hypoleuca</i>)	f			Gortlander (1987)
	f	f		Liffield <i>et al.</i> (1992)
great tit (<i>Parus major</i>)	f			Bengtsson & Rydén (1981)
	f			Sasvári (1990) (E)
blue tit (<i>Parus caeruleus</i>)			F	Slagsvold <i>et al.</i> (1994)
Lapland longspur (<i>Calcarius lapponicus</i>)			—	McLaughlin & Montgomerie (1985)
song sparrow (<i>Melospiza melodia</i>)		f		Smith & Merkt (1980)
white-throated sparrow (<i>Zonotrichia albicollis</i>)			—	Kopachena & Falls (1991) (E)
field sparrow (<i>Spizella pusilla</i>)	f			Best (1977)
medium ground finch (<i>Geospiza fortis</i>)			—	Price & Gibbs (1987)
red-winged blackbird (<i>Agelaius phoeniceus</i>)	m			Westneat <i>et al.</i> (1995)
common starling (<i>Sturnus vulgaris</i>)	—			Cotton & Wright (personal communication in Slagsvold (1997a))

preferentially (Slagsvold 1997a; table 1). Such differences may occur when the whole brood is still in the nest, when it is partially fledged, or when all the chicks have left the nest. It is possible that parentally biased favouritism when the brood is partially fledged reflects differences in the kind of care needed by nestlings and fledglings, but this seems unlikely in the earlier and later periods when all chicks are in, or out of, the nest. In general, differential feeding of different-sized offspring after leaving the nest is associated with brood division (see below; this applies to all the cases listed in table 1, except for blue tits *Parus caeruleus*, where this was not recorded; Slagsvold *et al.* (1994)).

- (ii) *The two parents feed different-sexed young differentially.* A number of studies suggest that the two parents differentially provision sons and daughters within a brood, usually with the female parent providing a higher proportion of the feeds to sons than to daughters

(Gowaty & Droge 1991; table 2). The only example known for nestlings is the eastern bluebird *Sialia sialis* (Gowaty & Droge 1991), with the remaining four examples being for fledglings and associated with brood division (see § 2).

- (iii) *The two parents feed individual young differentially.* Differential feeding of individual young has been most clearly demonstrated during the period after nest leaving, when it is known as brood division. Brood division is known in both nidifugous and nidicolous species (table 3), and in some cases can be complete, with individual chicks receiving care from only one parent. The division of chicks between the two parents may be related to their sex or size, but this is not always apparently so. A process analogous to brood division may occur during the nestling period. In great tits (*Parus major*), the two parents in each pair often feed from different positions on the nest rim (Kölliker *et al.* 1998), and this could lead

Table 2. A review of parentally biased favouritism in relation to chick sex in birds.

(Conventions for the letters in the body of the table are the same as for table 1. This table excludes studies in which differential reading by the two parents was analysed in relation to BSR rather than the sex of individual chicks (Clotfelter 1996; Nishiumi *et al.* 1996).)

species	sex of parent preferentially feeding male chick(s)		references
	nestling period	post-nestling period	
budgerigar (<i>Melopsittacus undulatus</i>)	—		Stamps <i>et al.</i> (1987) (C)
dunnock (<i>Prunella modularis</i>)		m	Byle (1990)
European robin (<i>Erithacus rubecula</i>)		f	Harper (1985)
eastern bluebird (<i>Sialia sialis</i>)	f		Gowaty & Droge (1991)
western bluebird (<i>Sialia mexicana</i>)	—		Leonard <i>et al.</i> (1994) (E)
blackbird (<i>Turdus merula</i>)		f	Snow (1958)
		f	T. Limbourg, personal communication
great tit (<i>Parus major</i>)	—		M. Kölliker, personal communication
snow bunting (<i>Plectrophenax nivalis</i>)		—	Lyon (personal communication in McLaughlin & Montgomerie (1985))
medium ground finch (<i>Geospiza fortis</i>)		—	Price & Gibbs (1987)
red-winged blackbird (<i>Agelaius phoeniceus</i>)	—		Teather (1992)
	—		Westneat <i>et al.</i> (1995)

Table 3. A review of studies with quantitative evidence for brood division in birds.

species	references
black coot (<i>Fulica atra</i>)	Horsfall (1984)
flamulated owl (<i>Otus flammeolus</i>)	Linkhart & Reynolds (1987)
northern mockingbird (<i>Mimus polyglottos</i>)	Zaia & Breitwisch (1989)
dunnock (<i>Prunella modularis</i>)	Byle (1990)
robin (<i>Erithacus rubecula</i>)	Harper (1985)
bluethroat (<i>Luscinia svecica</i>)	Anthonisen <i>et al.</i> (1997)
northern wheatear (<i>Oenanthe oenanthe</i>)	Moreno (1984)
blackbird (<i>Turdus merula</i>)	Edwards (1985)
American robin (<i>Turdus migratorius</i>)	Weatherhead & McRae (1990)
Lapland longspurs (<i>lapponica</i>)	McLaughlin & Montgomerie (1985)
song sparrow (<i>Melospiza melodia</i>)	Smith (1978), Smith & Merkt (1980)
white-throated sparrow (<i>Zonotrichia albicollis</i>)	Kopachena & Falls (1991)
medium ground finch (<i>Geospiza fortis</i>)	Price & Gibbs (1987)
cactus finch (<i>Geospiza scandens</i>)	Price & Gibbs (1987)
prairie warbler (<i>Dendroica discolor</i>)	Nolan (1978)

to the two parents feeding different sub-sets of the chicks defined by their position in the nest.

- (iv) *The two parents use different chick feeding rules.* There is now considerable evidence that the begging intensity of individual chicks influences the probability that the chick will be fed (Kilner & Johnstone 1997). In canaries (*Serinus canaria*), the parental response to chick begging posture varies with chick age and, more importantly, with the sex of the parent (R. M. Kilner, personal communication). Females pay decreasing attention to chick posture as the chicks grow older, whereas the responsiveness of males remains constant over the same range of chick ages. If individual chicks differ consistently in their begging behaviour, these chick feeding rules will result in the parents feeding different subsets of chicks, and may be the mechanism responsible for the differential feeding of different-sexed or -sized offspring described above.

The examples given above do not necessarily identify the chick characteristics discriminated for by the parents: in species with sexually size-dimorphic chicks, discrimination on the basis of size or sex will also tend to lead to preferential feeding in relation to the other of the two characteristics. Similarly, discrimination in relation to chick begging behaviour will lead to differential feeding of chicks that differ in their begging behaviour, and the reverse may also occur. Moreover, the cue that parents use to discriminate between chicks is not necessarily the characteristic that selects for parentally biased favouritism: for example, when some form of brood division is favoured by selection, the size or sex of chicks may be used as a convenient arbitrary cue identifying the subset of chicks that each parent should feed. However, the inability to identify the cues used by the parents, and the characters specifically responsible for selecting for parentally biased favouritism, are largely irrelevant in this context. What matters is that they suggest that parentally biased favourit-

ism may be widespread, and its occurrence requires a general explanation in terms of evolutionary advantage.

My main aim is, therefore, to investigate what kinds of selection pressure could account, in principle, for the two parents specializing in providing care to different offspring or different kinds of offspring. A number of hypotheses have been suggested in the past to account for various specific examples of parentally biased favouritism (McLaughlin & Montgomerie 1985; Gottlander 1987; Gowaty & Droge 1991; Slagsvold 1997a), but these have generally been framed verbally or graphically, and there is a need for mathematical models examining whether selection pressures act in the way proposed. The models here are presented in as general a form as possible in terms of differences in costs and benefits between the two parents, but I highlight the ways in which the general models correspond with previous specific hypotheses. In this context, only models explaining parentally biased favouritism in terms of current selective advantage are included: other models explaining parentally biased favouritism in terms of evolutionary history or selection at an earlier stage in the life history (Slagsvold 1997a) should be considered as alternative explanations in any empirical study.

2. THE MODELS

The models presented here are based on the two fundamental life-history trade-offs (Lessells 1991). The first of these is the trade-off between the number and fitness of offspring (Lack 1947). In the models presented, it is assumed that this trade-off occurs solely because care is 'depreciable' (*sensu* Clutton-Brock 1991), so that only one offspring benefits from each unit of care provided. As a result, the fitness that the parents gain through each offspring depends only on the amount of care that it receives and not on the care given to other offspring. The trade-off is incorporated into the models as the relationship between the fitness that the parents gain through each offspring (S_a and S_b , where the subscripts refer to different types of offspring) and the total care that the offspring receives (x_a and x_b , respectively) (figure 1a; Smith & Fretwell 1974). The shape of this relationship is determined by the complete range of ecological and physiological selection pressures acting on the offspring, and may include factors as diverse as metabolic rate, the usefulness of accumulated reserves, and the effect of final body size on the ability to compete with conspecifics and avoid predators. Differences in the biology of different types of offspring are therefore encapsulated in differences in these offspring fitness curves. However, despite the range of biological factors represented, all offspring fitness curves are expected to show diminishing fitness returns at higher levels of parental care (Smith & Fretwell 1974; Ratnieks 1996). It is assumed throughout that the offspring fitness curves increase monotonically, but at a decelerating rate.

The second life-history trade-off incorporated into the models is the 'cost of reproduction' (Williams 1966): in iteroparous species an increase in parental investment in the current family may reduce future survival and fecundity, and hence fitness accrued through future families ('residual fitness'). This trade-off is incorporated into the models as the relationship between the reduction in residual fitness (P_M and P_F , respectively, for male and female parents)

Figure 1. The evolutionarily stable distribution of parental care when the offspring differ in the benefits of care and the parents differ in the costs of care. (a) The relationship between the fitness accrued through an offspring ($S(x)$) and the amount of care that it receives for offspring of type 'a' (solid line) and type 'b' (dashed line) (the 'offspring fitness functions'). (b) The relationship between each parent's loss in residual fitness ($P(c)$, the cost of parental care) and the amount of care given by that parent for parent 1 (solid line) and parent 2 (dashed line) (the 'parental fitness functions'). The evolutionarily stable amounts of care (indicated by filled circles) were found by solving equation (2.9), and illustrate the equality of the marginal rates (graphically, the slopes of the tangents to the curve) at the ESS. The evolutionarily stable amounts of care shown assume that each family consists of one type a and one type b offspring. Functions shown are $S_a(x_a) = 1 - \exp(-(x_a - 1))$, $S_b(x_b) = 1 - \exp(-0.5(x_b - 1))$, $P_1 = 0.01c_1^2$, $P_2 = 0.02c_2^2$. For these functions, A^* (the evolutionarily stable amount of care given to offspring a) = 3.299, B^* (the evolutionarily stable amount of care given to offspring b) = 4.213, c_1^* (the evolutionarily stable amount of care given by parent 1) = 5.008, and c_2^* (the evolutionarily stable amount of care given by parent 2) = 2.504.

below that expected when no parental care is given to the current family (V_M and V_F , respectively) in relation to the parental effort made by the parent to the current family (e_M and e_F , respectively) (i.e. the residual fitnesses are $V_M - P_M(e_M)$ and $V_F - P_F(e_F)$, respectively; figure 1b). As is the case for the offspring curves, these parental fitness curves encompass all aspects of the biology of male and female parents that affect the way that parental effort affects residual fitness. The models do not explicitly include the effects of parental care in the current family to fitness accrued through other current reproductive opportunities (for instance, through polyandry, polygyny or mixed reproductive strategies) or to benefits to residual fitness (for instance, through sexual selection; e.g. Freeman-Gallant 1997). However, provided that these additional costs and benefits depend only on the total amount of care given by the parent, they can be incorporated as an increase or decrease in the cost of reproduction, and should therefore not qualitatively alter any conclusions regarding the evolution of parentally biased favouritism. Throughout, it is assumed that the parental fitness curve (the cost of reproduction in terms of the loss in residual fitness) is monotonically increasing at an increasing rate.

Models considering the evolution of parental care are complicated by the widespread occurrence of evolutionary conflicts of interest within families (Parker *et al.* 2002). Parent-offspring conflict occurs because each offspring is

more related to itself than its siblings in current and future families and is therefore selected to demand more care than would maximize its parents' fitness (Trivers 1974; Lessells & Parker 1999). Sexual conflict over parental care occurs because each parent accrues fitness through the care provided by both itself and its partner, but only pays the costs of its own efforts, so each is selected to give less care than would maximize its partner's fitness (Trivers 1972; Houston & Davies 1985; Lessells 1999). In general, modelling the outcome of such conflicts of interest requires the use of evolutionary game theory, and the outcome predicted will depend on the range of strategies open to each player, and in particular, in the case of parent-offspring conflict, on whether it is the parent or offspring that controls the distribution of care (see Mock & Parker 1997). In the first three models presented, it is assumed that the parent has complete control (i.e. the conflicting interests of the offspring are completely ignored). Later models (labelled as 'sib competition and parent-offspring conflict' models) give the control of the distribution of care to dominant offspring, but consider possible counter-strategies by the parents. All of the models include sexual conflict. In most models, the two parents care together for the offspring and each controls the amount (and usually also distribution) of its own care, but not that of its partner (Houston & Davies 1985). In later models (labelled 'sexual conflict' models), control is given to one of the two parents who can use pre-emptive desertion to choose the number and type of chicks for which it cares, while each parent then controls the amount of care that it gives to the offspring in its guardianship.

In general, the models presented assume the composition of the current family in terms of the number and type of offspring, and do not ask whether a different family size would have been evolutionarily stable (Houston & Davies 1985; Godfray & Parker 1991, 1992; Rodríguez-Gironés 1996; Smith & Härdling 2000) or whether parents are selected to terminate investment in some offspring (O'Connor 1978; Maynard Smith 1980; Haig 1990; Forbes 1993).

Models similar to some of those presented have previously been developed to investigate the evolution of parentally biased favouritism with respect to offspring sex (Lessells 1998). Such models have to take into account that the total fitness of all sons in the population is constrained to equal the total fitness of all daughters. The resultant Fisherian frequency dependence means that fitness benefits depend on the investment strategies of all individuals in the population, and not just on those of the two parents. The models presented do not include such frequency dependence and therefore apply where the fitness of different types of offspring does not depend on their abundance in the population as a whole.

As in many previous models of parental investment, these models make the simplifying assumptions that the parents each make a single investment decision rather than a series of investment decisions. Unless care has independent additive effects on fitness (Godfray 1995), dynamic programming models should be used to take into account the effect of an investment decision in one period on the consequences of decisions in succeeding periods (Mangel & Clark 1988; Clark & Ydenberg (1990) is a notable example for parental care). Repeated interaction

between the two parents and offspring also allows additional strategies such as punishment by the parents of selfish offspring behaviour (Clutton-Brock & Parker 1995; Godfray 1999). Moreover, the models presented here assume that the parents' investment decisions are 'sealed bids', made without prior knowledge of their mate's investment decision and not open to change once their mate's behaviour is known. The evolutionarily stable levels of care are altered when the parents can negotiate an outcome on a behavioural time-scale (McNamara *et al.* 1999). Despite these limitations, the models presented make these simplifying assumptions in an attempt to gain some initial insights into the selection pressures involved in the evolution of parentally biased favouritism.

(a) Parents differ in the cost of reproduction

One of the most frequent notions underlying previous hypotheses for parentally biased favouritism is that only the parent investing more overall can afford to invest in offspring of low reproductive value (Gottlander 1987; Slagsvold 1997a; Kölliker *et al.* 1998). For instance, Slagsvold (1997a) states in his 'life-history trade-off hypothesis' that 'A sexual difference may exist in the priority of parental investment in current versus future reproduction. If one parent (e.g. the female) invests more than its mate in the current family, this parent may put relatively more effort into the care of late hatching chicks, which often have low survival prospects.' I take this to mean that differences in the cost of reproduction between the sexes select for higher investment by one sex of parent, and that this in turn selects for that parent to care for offspring of lower reproductive value than does its partner.

In modelling this hypothesis I assume, for the sake of simplicity, that there are only two types of offspring (denoted by subscripts a and b), and that each family contains one of each type. Changing the family size, or the proportion of different types of offspring in the family, alters the precise allocation of care, but does not alter the qualitative conclusions of the model (see Maynard Smith 1980; Lessells 1998), provided that this does not result in selection for brood reduction.

Given these assumptions, the fitness of each of the parents (W_M and W_F for the male and female, respectively) is the sum of the fitness received through each offspring and its own residual fitness:

$$W_M = S_a(x_a) + S_b(x_b) + V_M - P_M(e_M) \quad (2.1)$$

and

$$W_F = S_a(x_a) + S_b(x_b) + V_F - P_F(e_F). \quad (2.2)$$

Denoting the care received by each offspring from each parent as a_M or a_F , and b_M or b_F , respectively, for offspring of type a and b, where subscripts indicate the sex of the parent, and assuming that parental effort, e_M and e_F , respectively, for male and female parents, is the sum of the parental care given by that parent, equations (2.1) and (2.2) can be rewritten as

$$W_M = S_a(a_M + a_F^*) + S_b(b_M + b_F^*) + V_M - P_M(a_M + b_M) \quad (2.3)$$

and

$$W_F = S_a(a_M^* + a_F) + S_b(b_M^* + b_F) + V_F - P_F(a_F + b_F), \quad (2.4)$$

where an asterisk indicates values of a and b for the other member of the pair. The investment by each parent in offspring of each type is evolutionarily stable when an individual cannot increase its own fitness by making a different investment, i.e. when W is maximized given the behaviour of its mate. The evolutionarily stable care by males and females in the two types of offspring can therefore be found by solving the equations $\partial W_M/\partial a_M = 0$, $\partial W_M/\partial b_M = 0$, $\partial W_F/\partial a_F = 0$ and $\partial W_F/\partial b_F = 0$, where $a_M = a_M^*$, $b_M = b_M^*$, $a_F = a_F^*$ and $b_F = b_F^*$, and checking that $\partial^2 W_M/\partial a_M^2 < 0$, $\partial^2 W_M/\partial b_M^2 < 0$, $\partial^2 W_F/\partial a_F^2 < 0$ and $\partial^2 W_F/\partial b_F^2 < 0$ at $a_M = a_M^*$, $b_M = b_M^*$, $a_F = a_F^*$ and $b_F = b_F^*$. These equations are

$$(\partial W_M/\partial a_M)^* = S'_a(A^*) - P'_M(M^*) = 0, \quad (2.5)$$

$$(\partial W_M/\partial b_M)^* = S'_b(B^*) - P'_M(M^*) = 0, \quad (2.6)$$

$$(\partial W_F/\partial a_F)^* = S'_a(A^*) - P'_F(F^*) = 0 \quad (2.7)$$

and

$$(\partial W_F/\partial b_F)^* = S'_b(B^*) - P'_F(F^*) = 0, \quad (2.8)$$

where primes denote the first derivatives of the functions S_a , S_b , P_M and P_F , and $A^* = a_M^* + a_F^*$, $B^* = b_M^* + b_F^*$, $M^* = a_M^* + b_M^*$, and $F^* = a_F^* + b_F^*$. If, as seems biologically plausible (Smith & Fretwell 1974), the offspring fitness functions S_a and S_b represent diminishing returns with increasing parental care (i.e. the second derivatives are negative), the second partial differentials will also be negative, and the values of A^* , B^* , M^* and F^* given by equations (2.5)–(2.8) will be evolutionarily stable. Similar stability considerations apply to the remaining models presented.

Equations (2.5)–(2.8) can be cross-substituted to yield

$$S'_a(A^*) = S'_b(B^*) = P'_M(M^*) = P'_F(F^*). \quad (2.9)$$

In other words, the evolutionarily stable pattern of parental care by two parents, in two different kinds of offspring, occurs graphically when the slopes of the two offspring and two parental fitness curves are equal. This is subject to the constraint that the total care received by the two offspring equals the total care given by the two parents (i.e. $A^* + B^* = M^* + F^*$) (figure 1). Thus, it is the marginal value of an offspring, not its total value, that determines which offspring should receive care (Haig 1990; Godfray 1995). Notably, equations (2.5)–(2.8) specify only the total amount of care received by each offspring and total amount of care given by each parent, but not the amount given by each parent to each kind of offspring. Essentially this means that, given the total amount of care to be divided between the offspring (over which there is sexual conflict), the parents agree evolutionarily as to its allocation between offspring (as argued verbally by Smiseth *et al.* (1998)).

The above analysis leads to a number of conclusions. First, the model may predict that different kinds of offspring receive different amounts of investment and/or have different reproductive values. As noted by Maynard Smith (1980) and Temme (1986), the qualitative expectations depend on the mathematical form of the offspring fitness functions. For example, under the exponential offspring fitness curves illustrated in figure 1, the type b offspring receives more care but has lower fitness at the ESS than

the type a offspring. There is thus a negative correlation between the amount of care that an offspring receives and its reproductive value. Under other offspring fitness functions, the amount of care received by the type b offspring can be less than that received by the type a offspring, although the resultant fitness of the type b offspring is usually less than that of the type a offspring (figure 2). These predictions emphasize that the reproductive value of different types of offspring is an outcome of selection (as, too, is the amount of care given to each offspring) and not a constraining selection pressure (as is the shape of the offspring fitness curve), contrary to the wording of some verbal hypotheses for parentally biased favouritism. The model shows that the amount of care may be positively or negatively associated with reproductive value across different types of offspring, depending on the relationship between the offspring fitness curves (figure 2).

Second, as implied by previous authors, the parent for whom care is more costly (in the sense that the cost of reproduction curve is steeper) is expected to provide less care overall to the offspring. (In addition, this parent actually pays a cost that is smaller than the other parent, with the fitness curves assumed in figure 1, although this may not be true when the parental fitness curves have a different form, in a manner analogous to the offspring fitness curves in figure 2.) This emphasizes that the actual cost paid ($P(a^* + b^*)$) is an outcome of selection, whereas it is the relationship between the loss in residual fitness and the amount of care given that is the constraining selection pressure. Because this curve can also be referred to as the 'cost of reproduction', care is needed over which of these two is being referred to. However, contrary to previous speculations, the model does not predict that care by the parent giving less care is concentrated on the offspring of higher reproductive value. As noted earlier, the model predicts only the total amount of care received by each type of offspring and given by each parent, but not the relative contributions by each parent to each offspring. These results can be understood intuitively by considering a parent with one (small) unit of care to invest in one of two offspring at different points on their respective fitness curves. What matters to the parent in evolutionary terms is not the current expected fitness value of each offspring, but the amount by which this will be increased when either of the offspring receives the unit of care. Graphically, this is the offspring that is located at a steeper point on its fitness curve, and will be the same offspring for both parents. If the parents continue to invest, they should continue to give their care to the offspring offering the best rate of return from each additional unit of investment. When the offspring fitness curves represent diminishing returns this will eventually lead to a situation in which the offspring offer equally good returns, and the parents become indifferent as to which offspring receives their care as long as this remains the case. This explains why the two offspring curves have the same slope at the ESS. Similarly, each parent should only continue to make further investments while the benefit accrued from a unit of care exceeds the cost to its own residual fitness of doing so. This explains why the offspring and parent fitness curves have the same slope at the ESS.

Finally, although this model does not explain parentally biased favouritism, it does not provide any selection

Figure 2. The effect of the relative forms of the offspring fitness functions for type a and type b offspring on the relative amounts of care received by, and fitness of, the two offspring types under the evolutionarily stable distribution of care. It is assumed that the fitness accrued through a given type of offspring is the same for the two parents. Then from equation (2.9), the slopes of the two offspring curves must be equal at the ESS. (a) The fitness curve for type b offspring is a constant multiple of that for type a offspring, so that the slope of the curve for type b offspring is also the same constant multiple of the slope for the type a offspring ($S'_b = uS'_a$). Since the slopes of both curves are decelerating, x_b^* must be less than x_a^* , and S_b less than S_a , at the ESS when $u < 1$. Thus, the relationship between the evolutionarily stable amount of care and the reproductive value of the offspring at the ESS is positive across offspring types. The offspring fitness functions are $S_b(x_b) = uS_a(x_a)$, evolutionarily stable care received is $x_a^* > x_b^*$, and offspring fitness at ESS is $S_a > S_b$. (b) The fitness curve for type b offspring is the same as that for type a offspring receiving less care by a constant amount v . Thus, the slopes are equal when x_b^* is v greater than x_a^* , and the fitness of the offspring is equal at the ESS. The offspring fitness functions are $S_b(x_b) = S_a(x_a + v)$, evolutionarily stable care received is $x_a^* < x_b^*$, and offspring fitness at ESS is $S_a = S_b$. There is no relationship between evolutionarily stable care and reproductive value across chick types. (c) The fitness curve for type b offspring is a constant amount, w , lower than that for type a offspring. Thus, the slopes are equal when x_b^* equals x_a^* , and the fitness of type b offspring is w lower than that of type a offspring at the ESS. The offspring fitness functions are $S_b(x_b) = S_a(x_a) - w$, evolutionarily stable care received is $x_a^* = x_b^*$, and offspring fitness at ESS is $S_a > S_b$. There is no relationship between evolutionarily stable care and reproductive value across chick types.

against it when it is advantageous for other reasons. Thus, when other models indicate that it is selectively advantageous to one or both parents for the parents to feed different individual offspring, the use of characters such as size as convenient arbitrary cues to discriminate between individual offspring would not invoke adverse selection. Equally, differences between the kinds of offspring cared for by each parent resulting from phylogenetic ancestry would not be selected against.

A slightly different form of the above hypothesis has been suggested by Slagsvold (1997a) for when the brood is divided between the parents. He asserts that it is 'in the interest of both sexes that the more care-giving parent takes responsibility for the largest and most valuable chicks.' If a brood of two offspring is divided between the parents

$$W_P = S_P(c_P) + S_Q(c_Q) + V_P - P_P(c_P), \quad (2.10)$$

where subscript P refers to the parent and the offspring in its care, and subscript Q refers to the other parent and the offspring in the other parent's care. The evolutionarily stable amount of care by the parent, c_P^* , is then given by

$$\partial W_P / \partial c_P = S'_P(c_P^*) - P'_P(c_P^*) = 0. \quad (2.11)$$

Thus, the evolutionarily stable care that a parent gives depends only on the fitness functions of itself and the offspring in its care, whereas the fitness that it gains depends additionally on these functions for the other offspring and parent. Table 4a gives an example for specific offspring and parent fitness functions. For a given cost of reproduction curve, a parent provides more care, but the offspring still has lower fitness, when the offspring in its care has lower fitness for a given amount of care (here a lower value of t , where $S(c) = 1 - \exp(-t(c-1))$). (As before, this result depends on the form of the offspring fitness curve; see figure 2.) Overall, the two offspring have higher combined fitness when the parent with the lower cost of reproduction curve (here a lower value of k , where $P(c) = kc^2$) cares for the offspring with the lower fitness curve. However, whereas parent 2 (with the steeper cost of reproduction curve) has higher fitness with this distribution of offspring (1.507 versus 1.396; table 4a), parent 1 has higher fitness with the reverse distribution of offspring (1.500 versus 1.514). Thus, the parents do not necessarily, as Slagsvold (1997a) states, agree over the distribution of chicks. The outcome of this sexual conflict is discussed further in § 2f.

Table 4. Parental fitness when the benefits of care differ between the offspring and/or costs of care differ between the parents. (Offspring fitness, $S_s(x_s) = (1 - \exp(-t_s(x_s - 1)))$). The cost of reproduction, $P_P = k_P c_P^2$. When parents care separately for each chick, the fitness of each parent, $W_P = (1 - \exp(-t_P(c_P - 1))) + (1 - \exp(-t_Q(c_Q - 1))) + V_P - k_P c_P^2$, where subscript P refers to the parent itself and subscript Q to its mate. From equation (2.11), the evolutionarily stable amount of care by the parent, c_P^* , is given by $t_P \exp(-t_P(c_P^* - 1)) = 2k_P c_P^*$. When parents care together for the two chicks, $W_P = (1 - \exp(-t_a(a_P + a_Q - 1))) + (1 - \exp(-t_b(b_P + b_Q - 1))) + V_P - k_P c_P^2$. From equation (2.9), the evolutionarily stable amount of parental care by the parent is given by $t_a \exp(-t_a(A^* - 1)) = t_b \exp(-t_b((C^* - A^*) - 1)) = 2k_1 c_1^* = 2k_2 c_2^*$, where A^* is the evolutionarily stable total amount of care to chick 'a' and $C^* = c_1^* + c_2^*$. Values in bold type denote the highest fitness for each of the two parents. In (d) the parents have the same fitness irrespective of whether the brood is divided or not.)

	evolutionarily stable care provided		offspring fitness at ESS		cost of reproduction at ESS	net fitness gain of parent at ESS
	c_P^*	$c_P^* + c_Q^*$	S_P^*	$S_1^* + S_2^*$	P_P^*	$W_P - V_P = S_P^* + S_Q^* - P_P^*$
(a) offspring differ in the benefits of care ($t_1 = 1, t_2 = 0.5$) and parents differ in the cost of care ($k_1 = 0.01, k_2 = 0.02$)						
parent 1 caring for chick 1 and parent 2 caring for chick 2	3.624		0.927	1.645	0.131	1.514
parent 1 caring for chick 2 and parent 2 caring for chick 1	4.451		0.822	1.698	0.198	1.500
parent 1 caring for both chicks and parent 2 caring for both chicks	5.010	7.515		1.069	0.251	0.818
parent 1 caring for chick 1 and parent 2 caring for chick 2	2.505				0.126	0.943
(b) offspring differ in the benefits of care ($t_1 = 1, t_2 = 0.5$) but parents have the same costs of care ($k_1 = k_2 = 0.01$)						
parent 1 caring for chick 1 and parent 2 caring for chick 2	3.624		0.927	1.749	0.131	1.618
parent 1 caring for chick 2 and parent 2 caring for chick 1	4.451		0.822	1.698	0.198	1.551
parent 1 caring for both chicks and parent 2 caring for both chicks	4.451		0.822	1.698	0.198	1.551
parent 1 caring for chick 1 and parent 2 caring for chick 2	3.624		0.927		0.131	1.618
parent 1 caring for both chicks and parent 2 caring for both chicks	3.975	7.959		1.741	0.158	1.582
parent 1 caring for chick 1 and parent 2 caring for chick 2	3.975				0.158	1.582
(c) offspring have the same benefits of care ($t_1 = t_2 = 1$) but parents differ in the costs of care ($k_1 = 0.0.1, k_2 = 0.02$)						
parent 1 caring for chick 1 and parent 2 caring for chick 2	3.624		0.927	1.803	0.131	1.672
parent 1 caring for chick 2 and parent 2 caring for chick 1	3.091		0.876		0.191	1.612
parent 1 caring for both chicks and parent 2 caring for both chicks	4.534	6.801		1.818	0.206	1.613
parent 1 caring for chick 1 and parent 2 caring for chick 2	2.267				0.103	1.716
(d) offspring have the same benefits of care ($t_1 = t_2 = 1$) and parents have the same costs of care ($k_1 = 0.0.1, k_2 = 0.01$)						
parent 1 caring for chick 1 and parent 2 caring for chick 2	3.624		0.927	1.854	0.131	1.724
parent 1 caring for chick 2 and parent 2 caring for chick 1	3.624		0.927		0.131	1.724
parent 1 caring for both chicks and parent 2 caring for both chicks	3.624		7.428	1.854	0.131	1.724
parent 1 caring for chick 1 and parent 2 caring for chick 2	3.624				0.131	1.724

(b) Parents differ in the benefits from different types of offspring

In the first model, it was assumed that the two parents received identical fitness benefits from any offspring, but

this may not always be the case. For instance, extra-pair paternity may reduce the benefit that the male accrues. Gottlander (1987) suggested that as a result 'the female can afford to invest more in lighter nestlings than the male

since she is totally confident in her maternity'. Both Liffield *et al.* (1992) and Slagsvold (1997a) subsequently interpreted Gottlander's explanation as an assumption that lighter chicks have a higher probability of extra-pair paternity, although it can also be read as meaning that females receive a higher benefit on average and can therefore afford to invest in low-value chicks. This interpretation is a slightly different version of the argument that the parent with the lower costs can afford to invest in lower-value chicks (see § 2a). Westneat *et al.* (1995) also proposed that the male should reduce his investment in individual chicks that were more likely to have resulted from cuckoldry. In addition to size, they also suggested that males might use offspring sex as a cue to the likelihood of extra-pair paternity (if females biased the sex of extra-pair young towards males; see Sheldon & Ellegren 1996). A similar interaction between offspring type and parental sex on the net benefit accrued through chicks has been proposed by Gowaty & Droge (1991), but resulting from cooperative or competitive behaviour expressed more strongly by one sex of offspring and experienced more strongly by one sex of parent, rather than from extra-pair paternity (see Lessells 1998). These hypotheses differ in whether the proportional reduction in fitness experienced by one parent is the same for all types of offspring (as Gottlander seems to suggest), or varies between them (as the other authors clearly state).

Differences between the parents in the fitness accrued through offspring can be modelled by making the fitness accrued to the male from each type of offspring a constant multiple, p_a and p_b , respectively for the two offspring types, of the fitness that the female accrues through the same offspring ($S_{a,F}$ and $S_{b,F}$, respectively). The fitness of the parents is then

$$W_M = p_a S_{a,F}(a_M + a_F^*) + p_b S_{b,F}(b_M + b_F^*) + V_M - P_M(a_M + b_M) \quad (2.12)$$

and

$$W_F = S_{a,F}(a_M^* + a_F) + S_{b,F}(b_M^* + b_F) + V_F - P_F(a_F + b_F), \quad (2.13)$$

and the evolutionarily stable pattern of parental care given by

$$(\partial W_M / \partial a_M)_* = p_a S'_{a,F}(A^*) - P'_M(M^*) = 0, \quad (2.14)$$

$$(\partial W_M / \partial b_M)_* = p_b S'_{b,F}(B^*) - P'_M(M^*) = 0, \quad (2.15)$$

$$(\partial W_F / \partial a_F)_* = S'_{a,F}(A^*) - P'_F(F^*) = 0 \quad (2.16)$$

and

$$(\partial W_F / \partial b_F)_* = S'_{b,F}(B^*) - P'_F(F^*) = 0. \quad (2.17)$$

If the proportional reduction in fitness benefit is the same for all types of offspring (i.e. $p_a = p_b = p$), as Gottlander (1987) appears to suggest, then equations (2.14)–(2.17) reduce to

$$S'_{a,F}(A^*) = S'_{b,F}(B^*) = (1/p)P'_M(M^*) = P'_F(F^*). \quad (2.18)$$

In other words, reducing the fitness accrued by the male from all types of offspring by a constant multiple, p , has the same effect on the evolutionarily stable parental care as increasing the male's cost of reproduction by a constant multiple $1/p$ (cf. equations (2.9) and (2.18)). This means

that the conclusions reached above from the previous model also apply here, and a proportional reduction in the fitness benefit accrued by one parent that is constant across offspring types cannot explain parentally biased favouritism. It also emphasizes the point made above that verbal arguments based on the reproductive value of different types of offspring relative to the total care provided by each parent are misleading.

The case in which the proportional reduction is not the same across all offspring types can be investigated further by substituting equation (2.14) into equation (2.15),

$$S'_{a,F}(A^*)/S'_{b,F}(B^*) = p_b/p_a, \quad (2.19)$$

and equation (2.16) into equation (2.17),

$$S'_{a,F}(A^*)/S'_{b,F}(B^*) = 1. \quad (2.20)$$

If p_a does not equal p_b then equations (2.19) and (2.20) cannot simultaneously be true. If p_a is greater than p_b and equation (2.20) is true, then for the male, the marginal rate of return from type a offspring ($p_a S'_{a,F}(A^*)$) is greater than that from type b offspring ($p_b S'_{b,F}(B^*)$) and he should invest only in type a offspring, while the female invests in both types of offspring. Conversely, if p_a is greater than p_b but equation (2.19) is true, then for the female the marginal rate of return from type a offspring ($S'_{a,F}(A^*)$) is less than that from type b offspring ($S'_{b,F}(B^*)$) and she should invest only in type b offspring, while the male invests in both types of offspring. Numerical analysis shows that there are also situations in which each sex of parent cares for only one type of offspring (figure 3).

Thus, differences in the benefits accrued through the offspring between the two parents can select for parentally biased favouritism, provided that the proportional difference in fitness between the parents is not the same for all offspring types. However, this creates a situation in which the marginal rates of fitness gain cannot be the same for each of the two types of offspring for both parents. One (or both) of the parents stops caring for the type of offspring that offers it the poorer investment option and an extreme form of parentally biased favouritism results in which some types of offspring are cared for by only one of the two parents. In all the examples given in tables 1 and 2, differential feeding by the two parents of different kinds of offspring is much less distinct.

Further investigation of the pattern of parentally biased favouritism predicted by this model can be carried out numerically. Figure 3 shows the predicted patterns of care when the offspring benefit curves are the same for type a offspring and both sexes of parents, and for type b offspring for female parents, whereas the fitness benefit to males from type b offspring is only half that to females (figure 3a). The costs of reproduction are assumed to be identical for the two parents (figure 3b). One biological situation that these assumptions could represent is when there are two kinds of offspring which the parents can discriminate between using some cue, which are identical in terms of the effects of care on their fitness, and where half of one group (the type b offspring) have extra-pair paternity (but the individual offspring affected are not identifiable by the parents). The frequency of extra-pair paternity is assumed to be unrelated in successive families of individual males (i.e. is restricted *sensu* Westneat &

Sherman (1993)). Under these assumptions, at least one of the types of offspring is cared for by only one parent, but whether it is the male who cares only for type a offspring, the female who cares only for type b offspring, or both, depends, among other parameters, on the proportion of type b offspring in the family. Figure 3c,d shows how the total care that individual offspring of each type receive, and the total care that each sex of parent gives, varies with the proportion of type b offspring in the family. When there are only type a offspring, the two parents provide an equal amount of care. With low proportions of type b offspring in the family, the male discriminates completely against these young and cares only for the type a offspring. The female, however, exactly compensates for

Figure 3. The evolutionarily stable distribution of care when parents differ in the benefits of care from given types of offspring. (a) The relationship between the fitness accrued through an offspring and the amount of care that it receives ($S(x)$) for type a and type b offspring and female parents, and type a offspring and male parents (solid line), and type b offspring and male parents (dashed line). (b) The relationship between each parent's loss in residual fitness (the cost of parental care, $P(x)$) and the amount of care given by that parent for both parents. (c) The evolutionarily stable amount of care given to each offspring of each type (dashed line refers to type b chicks), and (d) the evolutionarily stable amount of care given by each parent, in relation to the proportion of type b offspring in the family (dashed line relates to male). Functions shown in (a) are $S_{a,F}(x_a) = S_{a,M}(x_a) = 1 - \exp(-0.5(x_a - 1))$, $S_{b,F}(x_b) = 1 - \exp(-0.5(x_b - 1))$, and $S_{b,M}(x_b) = 0.5(1 - \exp(-0.5(x_b - 1)))$. Functions shown in (b) are $P_F(c_F) = 0.02c_F^2$ and $P_M(c_M) = 0.02c_M^2$. Thus, $W_F = N(1-p)(1 - \exp(-0.5((a_F + a_M^*)/(N(1-p)) - 1)) + N(1 - \exp(-0.5((c_F + c_M^* - a_F - a_M^*)/(Np) - 1)) + V_F - 0.02c_F^2$, and $W_M = N(1-p)(1 - \exp(-0.5((a_F^* + a_M)/(N(1-p)) - 1)) + 0.5N(1 - \exp(-0.5((c_F^* c_M - a_F^* - a_M)/(Np) - 1)) + V_M - 0.02c_M^2$, where a_F , a_M , c_F and c_M are the amounts of care by the female and male parent, respectively, in type a offspring in total and in the family in total, respectively, N is the family size, and p is the proportion of type b offspring in the family. Evolutionarily stable amounts of care are given (i) when the female cares for type a and b, and the male for type a, by the equations $\partial W_F/\partial a_F = 0$, $\partial W_F/\partial c_F = 0$, and $\partial W_M/\partial c_M = 0$ when $c_M = a_M$. Thus, $A^* = C^*(1-p)$, and $c_F^* = c_M^* = C^*/2 = 12.5\exp(-0.5((C^*/n - 1))$, where $A^* = a_F^* + a_M^*$ and $C^* = c_F^* + c_M^*$; (ii) when the female feeds type b and the male type a, by the equations $\partial W_F/\partial c_F = 0$ and $\partial W_M/\partial c_M = 0$ when $a_F = 0$ and $c_M = a_M$. Thus, $c_F^* = 12.5\exp(-0.5(c_F^*/(Np) - 1))$ and $c_M^* = 12.5\exp(-0.5(c_F^*/(Np) - 1))$; (iii) when the female cares for type b and the male for type a and b, by the equations $\partial W_F/\partial c_F = 0$, $\partial W_M/\partial c_M = 0$ and $\partial W_M/\partial a_M = 0$, when $a_F = 0$. Thus, $A^* = C^*(1-p) - \ln(0.5)Np(1-p)/0.5$ and $c_F^* = 2 c_M^* = 12.5\exp(-0.5((C^* - A^*)/(Np) - 1))$. Of these three patterns of care, the one that is evolutionarily stable is the one giving the highest values of both W_F^* and W_M^* . Values shown in (c) and (d) were calculated for $N = 4$.

the bias in the male's care so that until the point at which there are 50% type b offspring in the family the two types of offspring receive the same amount of care individually, and the two parents give the same total amount of care. At this point, the male cares exclusively for type a offspring and the female for type b offspring. As the proportion of type b offspring in the family increases further, the two parents continue each to care exclusively for one type of offspring, but the female now increases the total amount of care that she gives, while the male does the opposite. However, the increase in the number of type b offspring and decrease in type a offspring more than counteracts this. As a result, the care received by individual type b offspring decreases and that by individual type a offspring increases, eventually reaching a point where the type a and b offspring offer equally good investment opportunities to the male and he begins to care for both types of offspring. (Beyond this point the female provides a decreasing amount of care and type b chicks receive an increasing amount of care.) Thus, in families with a high proportion of type b offspring the male cares for both types of offspring and the female only for type b offspring.

Figure 4. The effect of offspring with extra-pair paternity on (a) the total care given by each parent and (b) the fitness of the parent. Predictions are for a model in which there are two types of chick with 0% (type a) or 50% (type b) extra-pair paternity. Predictions are made for the cases where the parents do (broken lines) or do not (solid lines) discriminate between type a and b chicks. Evolutionarily stable patterns of care when the parents discriminate were obtained as described in the caption to figure 3, and when they do not discriminate using equation (2.15), but assuming that type a and b chicks are identical and setting $p = 1 - 0.5$ (proportion of type b chicks in the brood). All other parameter values are the same as for figure 3. Abbreviations: F, females; M, males; B, both parents.

The figures showing total care received by each offspring and total care given by each parent are not symmetrical about 50% type b offspring in the family because the fitness benefits of the two types of offspring are not the inverse for the two sexes of parents. Had the curve representing the benefit of type a offspring to females been the same as that for type b offspring to males (and other relationships remained the same), the left-hand halves of figure 3c,d would have been mirror images of the right-hand halves. In addition, the constancy in the total care by each parent and the total care received by each individual offspring over the lower range of proportion of type b offspring in the family depends on the offspring benefit curves being identical for three of the four offspring type-parental sex combinations.

B. Kempenaers (personal communication) has pointed out that the above results may have implications for the evolution of discrimination against young with extra-pair paternity within broods by cuckolded males (Kempenaers & Sheldon 1996). Although the model predicts that males should discriminate against such offspring, it also predicts that over a substantial range of proportions of suspected extra-pair offspring in the family (0–50% in the example in figure 4), the female exactly compensates so that the care received by each offspring is unchanged from that when there are no illegitimate young. This seems to imply that any costs of discrimination (for instance, an increase in the amount of time deciding which offspring should be fed) would outweigh the benefits. However, if the male does not discriminate, the evolutionarily stable pattern of care should be calculated, taking into account the reduction in the benefit that he accrues as a result of the loss in paternity. In this

case, the male is predicted to decrease the amount of care to the family as the proportion of extra-pair young in the family increases, while the female increases the care that she gives, so that the amount of care that each offspring receives is lower when the male does not discriminate against suspect offspring (figure 4a). As a result, the fitness of the female is also reduced, but the male, remarkably, has higher fitness when he does not discriminate (figure 4b). The decrease in his cost of reproduction more than offsets the lower benefit through the offspring because the amount of care that he provides is sufficiently reduced. Does this mean that selection favours males who evolutionarily abandon an ability to discriminate illegitimate young? The answer under the 'single-shot sealed bid' assumption of the present models seems to be no. For any pattern of care by the female in which she receives equal marginal gains from legitimate and suspect offspring, the male has higher fitness if he provides his care discriminately, so indiscriminate care is not evolutionarily stable. The male is condemned to evolve discrimination that will lead, in evolutionary time, to an increase in his care, a decrease in his mate's care and a decrease in his own fitness. It would be interesting to know whether this would still be the case if the responses in levels of care occurred on a behavioural time-scale. Models of evolutionarily stable negotiation rules (McNamara *et al.* 1999) might be particularly enlightening here.

In the model presented, it is assumed that there are only two types of offspring. However, in many cases, there will be as many types of offspring (as defined by their fitness curves) as there are young in the family. Offspring are only cared for by both parents when the slopes of the benefit curves for that offspring type for each of the two parents are the same at the evolutionarily stable amount of care. If the ratios of the slopes of the benefit curves for the two parents vary between offspring types, then, in general, this can only be true for one of the offspring types and all other types of offspring will be cared for by only one of the parents.

(c) Parents differ in the effort incurred in giving care to different types of offspring

In the first model, it was assumed that the cost of care to the parents depends only on the total amount of care that the parents give, and not on the identity of the beneficiary. However, this will not be the case if the effort involved in providing care is greater for some kinds of offspring. For instance, the transfer of food to smaller nestlings may take more time. This time may represent an increase in effort for a parent who would otherwise be absent from the nest, but not for a parent who would otherwise be present. (This, of course, begs the question, why a difference in nest attendance exists.) Stamps *et al.* (1985) suggested that this might explain why female budgerigars selectively seek out and feed the smallest chicks in the family.

Differences between the parents in the effort involved in caring for different kinds of offspring can be modelled by making the parental effort of the male, e_M , the sum of the products of a constant, q_a and q_b , respectively for type a and b offspring, and the care provided to each of the two offspring types. The fitness of the parents is then

$$W_M = S_a(a_M + a_F^*) + S_b(b_M + b_F^*) + V_M - P_M(q_a a_M + q_b b_M) \quad (2.21)$$

and

$$W_F = S_a(a_M^* + a_F) + S_b(b_M^* + b_F) + V_F - P_F(a_F + b_F), \quad (2.22)$$

and the evolutionarily stable pattern of parental care given by

$$(\partial W_M / \partial a_M)_* = S'_a(A^*) - q_a P'_M(q_a a_M^* + q_b b_M^*) = 0, \quad (2.23)$$

$$(\partial W_M / \partial b_M)_* = S'_b(B^*) - q_b P'_M(q_a a_M^* + q_b b_M^*) = 0, \quad (2.24)$$

$$(\partial W_F / \partial a_F)_* = S'_a(A^*) - P'_F(F^*) = 0 \quad (2.25)$$

and

$$(\partial W_F / \partial b_F)_* = S'_b(B^*) - P'_F(F^*) = 0. \quad (2.26)$$

If the constant by which parental effort is increased in males is the same for all types of offspring (i.e. $q_a = q_b = q$), then equations (2.23)–(2.26) reduce to

$$S'_a(A^*) = S'_b(B^*) = q P'_M(q M^*) = P'_F(F^*). \quad (2.27)$$

In other words, increasing the parental effort in males by a constant multiple for all offspring types has the same effect as changing the relationship for the cost of reproduction in males (cf. equations (2.9) and (2.27)). Substituting equation (2.23) into equation (2.24)

$$S'_a(A^*) / S'_b(B^*) = q_b / q_a \quad (2.28)$$

and equation (2.25) into equation (2.26)

$$S'_a(A^*) / S'_{b,F}(B^*) = 1. \quad (2.29)$$

If q_a does not equal q_b , then equations (2.28) and (2.29) cannot simultaneously be true. If q_a is greater than q_b and equation (2.29) is true, then for the male the marginal rate of fitness gain from caring for type a offspring ($\partial W_M / \partial a_M$) is less than that from caring for type b offspring ($\partial W_M / \partial b_M$) and he should invest only in type b offspring, while the female invests in both types of offspring. Conversely, if q_a is greater than q_b , but (2.28) is true, then for the female the marginal rate of fitness gain from caring for type a offspring ($\partial W_F / \partial a_F$) is greater than that from caring for type b offspring ($\partial W_F / \partial b_F$) and she should invest only in type a offspring, while the male invests in both types of offspring.

The predicted effects of a difference in the effort involved in caring for different kinds of offspring between the sexes are therefore equivalent to those of a difference in the benefits accrued from caring for different kinds of offspring: differences in the effort involved in caring for offspring between the parents can select for parentally biased favouritism, provided that the proportional difference is not the same for all offspring types, but the favouritism is extreme, with some types of offspring being cared for by only one of the two parents.

(d) Sibling competition

The models so far have assumed that the distribution of care among the offspring is controlled entirely by the parents. Slagsvold (1997a) has suggested in his 'sibling rivalry hypothesis' that if the two parents deliver different amounts

of food to the nestlings from predictably different positions, and dominant chicks are able to control access to the food within each of these locations, the most dominant chick should choose the position where the parent feeds at the higher rate. The remaining chicks should choose the position offering them the best provisioning rate taking into account the parental feeding rate and the amount of competition from sibs. If dominance varies between chick types (for instance with chick size), different chick types may be fed differentially by the two parents. This parentally biased favouritism results from the behaviour of the chicks choosing the parents, rather than the reverse.

Slagsvold (1997a) provided an informal graphical model in which each successive chick in the hierarchy took up to a fixed amount of food, and concluded that the only consistent prediction was that the most dominant chick should be fed by the parent providing more food. However, a complete model needs to take into account a number of additional factors. First, dominant offspring are not expected to take a fixed amount of food, but rather an amount that depends on the total amount of food available, and on the number of subordinate sibs and their degree of relatedness (Parker *et al.* 1989). If there are two offspring, then the dominant offspring chooses how much food to take and how much to leave for the subordinate offspring. When there are three offspring, the alpha offspring chooses how much to take, and the beta offspring then chooses how much of the remainder to take. However, the pay-off to the alpha offspring of taking any given amount depends on how the beta offspring divides the remainder, while the way that the beta offspring does this depends on the amount taken by the alpha offspring. The model is therefore an evolutionary game between the alpha and beta offspring (Parker *et al.* 1989). As the family size increases, all but the lowest offspring in the dominance hierarchy are players in the game, and the model must solve for each of their strategies in terms of the amount of food that they leave for subordinates.

Second, even though the offspring are entirely in control of the distribution of food, the total amount of food provided (c_M and c_F , respectively for the male and female parent) is still under the control of the two parents. There is thus an evolutionary game between the offspring and each of the two parents. The pay-off that each of the parents receives depends not only on the amount of food that they provide, but also on how the offspring divide it up. The pay-off that each offspring receives depends not only on the amount of food that they take for their own consumption, but also on the total amount of food provided (and on the strategies of their sibs) (Forbes 1993).

If there are three full sibs (denoted by the subscripts α , β and γ), and the alpha and beta offspring take proportions of the food available to them of r_α and r_β , then the fitness of each of the parents and offspring is

$$W_M = S_\alpha(r_\alpha C) + S_\beta((1 - r_\alpha) r_\beta C) + S_\gamma((1 - r_\alpha)(1 - r_\beta)C) + V_M - P_M(c_M), \quad (2.30)$$

$$W_F = S_\alpha(r_\alpha C) + S_\beta((1 - r_\alpha) r_\beta C) + S_\gamma((1 - r_\alpha)(1 - r_\beta)C) + V_F - P_F(c_F), \quad (2.31)$$

$$W_\alpha = 2S_\alpha(r_\alpha C) + S_\beta((1 - r_\alpha) r_\beta C) + S_\gamma((1 - r_\alpha)(1 - r_\beta)C) + 1/2[V_M - P_M(c_M) + V_F - P_F(c_F)], \quad (2.32)$$

$$W_\beta = S_\alpha(r_\alpha C) + 2S_\beta((1 - r_\alpha)r_\beta C) + S_\gamma((1 - r_\alpha)(1 - r_\beta)C) + 1/2 [V_M - P_M(c_M) + V_F - P_F(c_F)], \quad (2.33)$$

and

$$W_\gamma = S_\alpha(r_\alpha C) + S_\beta((1 - r_\alpha)r_\beta C) + 2S_\gamma((1 - r_\alpha)(1 - r_\beta)C) + 1/2 [V_M - P_M(c_M) + V_F - P_F(c_F)], \quad (2.34)$$

where $C = c_M + c_F$. The evolutionarily stable pattern of care can, as usual, be found by solving the equations $\partial W_M/\partial c_M = 0$, $\partial W_F/\partial c_F = 0$, $\partial W_\alpha/\partial r_\alpha = 0$ and $\partial W_\beta/\partial r_\beta = 0$. Similar sets of equations can be written for a family of any size.

The above equations assume that the brood is undivided so that dominant offspring can simultaneously monopolize the care provided by both parents, but the essence of Slagsvold's (1997a) idea is that, because of the separate feeding positions of the two parents, individual chicks can only monopolize the care of one parent. If this is the case, the equations reflecting parental and offspring fitness must be rewritten taking into account this division. For instance, if the alpha offspring is fed by the male, and the beta and gamma offspring by the female, these equations become

$$W_M = S_\alpha(c_M) + S_\beta(r_\beta c_F) + S_\gamma((1 - r_\beta)c_F) + V_M - P_M(c_M), \quad (2.35)$$

$$W_F = S_\alpha(c_M) + S_\beta(r_\beta c_F) + S_\gamma((1 - r_\beta)c_F) + V_F - P_F(c_F), \quad (2.36)$$

$$W_\alpha = 2S_\alpha(c_M) + S_\beta(r_\beta c_F) + S_\gamma((1 - r_\beta)c_F) + 1/2 [V_M - P_M(c_M) + V_F - P_F(c_F)], \quad (2.37)$$

$$W_\beta = S_\alpha(c_M) + 2S_\beta(r_\beta c_F) + S_\gamma((1 - r_\beta)c_F) + 1/2 [V_M - P_M(c_M) + V_F - P_F(c_F)] \quad (2.38)$$

and

$$W_\gamma = S_\alpha(c_M) + S_\beta(r_\beta c_F) + 2S_\gamma((1 - r_\beta)c_F) + 1/2 [V_M - P_M(c_M) + V_F - P_F(c_F)]. \quad (2.39)$$

The evolutionarily stable pattern of care thus clearly depends on the distribution of offspring between the two parents. Slagsvold (1997a) assumes that this is under the control of individual chicks (i.e. chicks can prevent a subordinate chick from receiving food but cannot prevent it from being present at the feeding position). If this is the case, the evolutionarily stable distribution of offspring occurs when no offspring can benefit by moving to the other feeding position. This can be found by calculating the fitness gain of each offspring under the evolutionarily stable pattern of care (defined by the values of c and r) for each distribution of offspring. It should be noted from equations (2.35)–(2.39) that the partial differentials only contain terms for the r - and c -values of the offspring and parent in that feeding position. This means that, for a given distribution of offspring between the feeding positions, the evolutionarily stable strategies of the offspring and parent in each feeding position depend only on the behaviour of the parent and offspring at that feeding position.

Given the complexity of the equations defining the ESS, predictions are made here for specific mathematical functions (cf. Parker *et al.* 1989; Forbes 1993). It is assumed that the offspring have identical fitness functions, $S(x)$

$= (x - 1)/x$. Under this assumption the r -values are independent of the total amount of food to be divided (Forbes 1993; see table 5 for r -values with up to four offspring competing), greatly simplifying the analyses. The parental fitness curves are assumed to have the form $P = kc^2$, where k is a constant that determines the steepness with which the cost of reproduction increases with increasing parental care. Considering the way that the sibs divide food among themselves, and the parent's cost of reproduction, it is possible to specify the evolutionarily stable amount of care when there is any given number of sibs at a feeding position. This in turn allows the fitness of each of the offspring to be calculated (see table 5). If there is a single offspring, its fitness depends only on the value of k of the parent feeding it. Such an 'only' offspring having to choose between parents feeding in different positions should choose the parent with the less steep cost of reproduction.

If there are two sibs, their evolutionarily stable distribution depends on the values of k of the parents. When these values are equal, the fitness of an offspring is always higher when there is one offspring in each position than when they both feed at the same position, so the evolutionarily stable distribution of offspring is $\alpha : \beta$ ($= \beta : \alpha$, where the sibs written before the colon are fed by the parent with the less steep cost of reproduction (in the 'better' feeding position) and the offspring after the colon are fed by the other parent), because neither sib can gain by moving when they are alone at a feeding position. The situation is more complicated when the parents differ in their cost of reproduction. Figure 5a shows how the fitness of each offspring changes as the steepness of the cost of reproduction of the parent at the poorer position increases, while that of the parent at the better position is held constant. Because it is assumed that the better position is of constant quality, the fitness of the alpha and beta sibs remain constant if they feed together at this position. If they feed separately, however, the fitness of the offspring in the better position is higher than that of the other offspring, but the fitness of both offspring decreases as the quality of the poorer position decreases (the offspring in the better (constant) position gets a decreasing fitness benefit from its sib in the other position) (figure 5a). Consequently, there are three regions in terms of the ESSs depending on the quality of the poorer position (i.e. the steepness of the cost of reproduction of the parent feeding there).

The first of these occurs where there is little difference in the steepness of the cost of reproduction of the two parents (labelled as region 1 in figure 5a), and both offspring have a higher fitness if they feed separately than if they feed together. This means that it pays neither offspring to join the other, even if it is in the poorer position. Thus, there are two alternative ESSs: $\alpha : \beta$, with the alpha sib in the better position, and $\beta : \alpha$, with the alpha sib in the poorer position. Both of these ESSs is stable given the assumptions of the model. The question is whether other resolutions are possible on a behavioural time-scale. If both of the offspring are together in the better position, the beta offspring gets a larger increase in fitness by moving to the poorer quality position than does the alpha offspring, and might be more ready to move in a war of attrition between the two sibs over the better quality pos-

Table 5. The model of sibling competition and parent-offspring conflict (after Forbes 1993).

(The fitness benefit of an offspring to a parent as a function of the care received (x), $S(x) = 1 - 1/x$. $r_{\alpha,2}^*$, the evolutionarily stable value of r_α when there are two sibs competing is found by solving the equation $\partial(2(1 - 1/(r_\alpha C)) + (1 - 1/((1 - r_\alpha)C)) + 1/2(V_M - P(c_M) + V_F + P(c_F)))/\partial r_\alpha = 0$, where C is the total care provided, and setting $r_\alpha = r_{\alpha,2}^*$ (see Forbes 1993). This gives $r_{\alpha,2}^* = 0.586$. Because $r_{\alpha,2}^*$ is independent of C , 0.586 is the proportion of care taken whenever the deciding chick is dominant to one other chick, i.e. the penultimate chick in the hierarchy. Thus, the value of $r_{\beta,3}^*$ (when three sibs are competing) is also 0.586. $r_{\alpha,3}^*$, the evolutionarily stable value of r_α when there are three sibs competing can then be found by solving the equation $\partial(2(1 - 1/(r_\alpha C)) + (1 - 1/((1 - r_\alpha)0.586C)) + (1 - 1/((1 - r_\alpha)(1 - 0.586)C)) + 1/2(V_M - P(c_M) + V_F + P(c_F)))/\partial r_\alpha = 0$, and setting $r_\alpha = r_{\alpha,3}^*$. This gives $r_{\alpha,3}^* = 0.411$. Because $r_{\alpha,3}^*$ is independent of C , 0.411 is the proportion of care taken whenever the deciding chick is dominant to two other chicks, i.e. the last but two chicks in the hierarchy. Thus, the value of $r_{\beta,4}^*$ (when four sibs are competing) is also 0.411, and the value of $r_{\gamma,4}$ is 0.586. A similar process can then be used to solve for $r_{\alpha,4}^*$ and successive r_α -values (Forbes 1993). The proportion of care that each chick receives, p , is calculated from the relevant r -values. For example, in a group of three competing sibs $p_{\alpha,3} = r_{\alpha,3}$, $p_{\beta,3} = (1 - r_{\alpha,3})r_{\beta,3}$, and $p_{\gamma,3} = (1 - r_{\alpha,3})(1 - r_{\beta,3})$. The total fitness value of the competing sibs to the parent, $F(C)$, is simply the sum of the $S(x)$ -values for those sibs. For example, in a group of three competing sibs, $F(C) = (0.411C - 1)/(0.411C) + (0.345C - 1)/(0.345C) + (0.244C - 1)/(0.244C)$. The residual fitness of a parent giving c_P care = $V_P - kc_P^2$ (where the subscript 'P' denotes either parent). When only one parent cares for a group of sibs, $C = c_P$, so C_{one}^* , the evolutionarily stable value of C when one parent cares, can be found by solving the equation $\partial(F(c_P) + V_P - kc_P^2)/\partial c_P = 0$, and setting $c_P = C_{\text{one}}^*$. This is where $F'(c_P) - 2kc_P = 0$. For example, for three sibs this is where $9.43/c_P^2 - 2kc_P = 0$, which gives $c_P = (4.71/k)^{1/3} = C_{\text{one}}^*$. When two parents care for a group of sibs, the evolutionarily stable amount of care by one parent depends on the amount of care provided by the other, and hence on the other's cost of reproduction. Denoting the two parents by the subscripts 1 and 2, and either parent by subscript P, the evolutionarily stable amount of care by each parent can be found by solving the simultaneous equations $\partial W_1/\partial c_1 = 0$ and $\partial W_2/\partial c_2 = 0$, where $c_1 = c_1^*$ and $c_2 = c_2^*$. $W_P = F(c_1 + c_2) + V_P - k_P c_P^2$, so $\partial W_P/\partial c_P = F'(c_1 + c_2) - 2k_P c_P$. Eliminating $F'(c_1 + c_2)$ from the partial differential for each parent, $k_1^* c_1 = k_2^* c_2$, so that $c_2^* = c_1^* k_2/k_1$, and $c_1^* + c_2^* = c_1^* (k_1 + k_2)/k_2 = C_{\text{two}}^*$. Thus, where, for example, there are three competing sibs, $\partial W_1/\partial c_1 = 9.43(C_{\text{two}}^*)^2 - 2k_1 c_1^* = 9.43k_2^2/((k_1 + k_2)c_1^*)^2 - 2k_1 c_1^* = 0$. Rearranging this equation, $c_1^* = (9.43k_2^2/(2k_1(k_1 + k_2)^2))^{1/3}$. Substituting this into $C_{\text{two}}^* = c_1^* (k_1 + k_2)/k_2$, $C_{\text{two}}^* = (9.43(k_1 + k_2)/2k_1 k_2)^{1/3}$. When $k_1 = k_2 = k$, this is where $C_{\text{two}}^* = (9.43/k)^{1/3}$. When one parent cares for each group of sibs, the fitness of the parent is $W_P = F_P + F_Q + V_P - kc_P^2$, where F_P is the fitness through the group of sibs that it cares for, and F_Q is the fitness through any sibs cared for by the other parent. Values of F for given values of k can be calculated using the expressions for C_{one}^* and $F(C)$ given in the table. The fitness of each sib, $W_s = S_s(p_s C_s) + F_P + F_Q + 1/2(V_P - kc_P^2 + V_Q - kc_Q^2)$, where the subscript 's' denotes the chick itself. When two parents care for the group of sibs, the fitness of each parent is $W_P = F + V_P - k_P c_P^2$. Values of F for given values of k_1 and k_2 can be calculated using the expressions for C_{two}^* and $F(C)$ given in the table. The fitness of each sib, $W_s = S_s(p_s C_s) + F + 1/2(V_1 - k_1 c_1^2 + V_2 - k_2 c_2^2)$. Parent-offspring conflict: when the two parents care together for the chicks, and $k_1 = k_2 = k$, each has fitness $W_{P,\text{together}} = F(C_{\text{two}}^*) + V - P(C_{\text{two}}^*/2)$. Substituting for $F(C_{\text{two}}^*)$ and C_{two}^* using the expressions in the table, when brood size = 2, $W_{P,\text{together}} = 2 - 4.12/(4.12/k)^{1/3} + V - k((4.12/k)^{1/3}/2)^2$, and when brood size = 4, $W_{P,\text{together}} = 4 - 17/(17/k)^{1/3} + V - k((17/k)^{1/3}/2)^2$. When the two parents each care separately for half the brood, and $k_1 = k_2 = k$, each has fitness $W_{P,\text{apart}} = 2F(C_{\text{one}}^*) + V - P(C_{\text{one}}^*)$. Substituting for $F(C_{\text{one}}^*)$ and C_{one}^* using the expressions in the table, when brood size = 2, $W_{P,\text{apart}} = 2(1 - 1/(0.5/k)^{1/3} + V - k((0.5/k)^{1/3})^2)$, and when brood size = 4, $W_{P,\text{apart}} = 2(2 - 4.12/(2.06/k)^{1/3}) + V - k((2.06/k)^{1/3})^2$. Subtracting $W_{P,\text{together}}$ from $W_{P,\text{apart}}$ and simplifying, $W_{P,\text{apart}} - W_{P,\text{together}} = 0.062k^{1/3}$ for broods of two chicks and $0.169k^{1/3}$ for broods of four chicks. More generally, if $F_{\text{apart}} = m - i/C$ and $F_{\text{together}} = n - j/C$, then $C_{\text{one}}^* = (i/2k)^{1/3}$ and $C_{\text{two}}^* = (j/k)^{1/3}$, and $W_{P,\text{apart}} - W_{P,\text{together}} = (2m - n) - (3.15i^{2/3} - 1.25j^{2/3})k^{1/3}$. If parents divide care equally between the chicks, $m = (\text{brood size})/2$, $n = \text{brood size}$, $I = (\text{brood size})^2/4$, and $j = (\text{brood size})^2$, so that $W_{P,\text{apart}} - W_{P,\text{together}} = 0$, confirming the result for general functions when parents divide care equally as given in § 2e.)

number of competing sibs	evolutionarily stable proportion of remaining care taken			evolutionarily stable proportion of care received by chick				$F(C)$	evolutionarily stable care provided by	
	r_α^*	r_β^*	r_γ^*	p_α^*	p_β^*	p_γ^*	p^*		one parent	two parents
									C_{one}^*	C_{two}^*
1	—	—	—	1.000	—	—	—	$1-1/C$	$(0.5/k)^{1/3}$	$\left[\frac{(k_1+k_2)}{(2k_1k_2)}\right]^{1/3}$
2	0.586	—	—	0.586	0.414	—	—	$2-4.12/C$	$(2.06/k)^{1/3}$	$\left[\frac{(4.12(k_1+k_2))}{2k_1k_2}\right]^{1/3}$
3	0.411	0.586	—	0.411	0.345	0.244	—	$3-9.43/C$	$(4.71/k)^{1/3}$	$\left[\frac{(9.43(k_1+k_2))}{2k_1k_2}\right]^{1/3}$
4	0.315	0.411	0.586	0.315	0.286	0.234	0.165	$4-17.00/C$	$(8.50/k)^{1/3}$	$\left[\frac{(17.00(k_1+k_2))}{2k_1k_2}\right]^{1/3}$

ition. If so, when the alpha sib is in the poorer position, it might be able to cause the beta offspring to surrender the better feeding position by moving to join it. If this were

the case, $\alpha : \beta$ would be the commoner ESS occurring in nature.

In the second region, the alpha offspring has a higher

Figure 5. The evolutionarily stable distribution of full sibs between the two parental feeding positions when total brood size is (a) two or (b) three. It is assumed that parents provide food at two different positions, between which each sib has to choose. Within positions there is a strict linear dominance hierarchy among sibs, such that the most dominant chick takes a share of the food provided, followed by its immediate subordinate, and so on down the hierarchy. The amount of food provided at each position is determined by the parent feeding there and is the outcome of an evolutionary game between the parent, who determines the total amount of food, and offspring, who determine how it is divided among themselves. Details of the offspring and parent fitness curves assumed are given in table 5. The figures show the total fitness of chicks (including that accrued through their sibs) in relation to the cost of reproduction (given by k) of the parent in the poorer quality position. The other parent has a fixed cost of reproduction, $k = 0.01$. The solid curves are for chicks alone at a position (so that there is one chick at the other position in (a), and two in (b)). Note that the upper curve is correctly labelled for the poorer position in (b). This counterintuitive result occurs because the chick also accrues fitness from its sibs at the better position. Broken lines (dashed for the better position, dashes and dots for the poorer position) are for the dominant and subordinate chicks when there are two chicks at a position (and hence no chick at the other position in (a) and one chick at the other position in (b)). The fitness of the three chicks when all three are in the better position is shown by short sections of horizontal lines in (b). Fitness values were calculated as described in table 4 and § 2d. In (a), the ESSs are: (1) $\alpha : \beta$ or $\beta : \alpha$ (sibs before and after the colon are in the better and poorer patches, respectively); (2) $\alpha : \beta$; (3) $\alpha\beta : -$. In (b), the ESSs are: (1) $\beta\gamma : \alpha$ or $\alpha\gamma : \beta$; (2) $\alpha\gamma : \beta$; (3) $\alpha\beta : \gamma$ or $\alpha\gamma : \beta$; (4) $\alpha\beta : \gamma$, $\alpha\gamma : \beta$, or $\beta\gamma : \alpha$; (5) $\alpha\beta : \gamma$ or $\alpha\gamma : \beta$; (6) $\alpha\beta : \gamma$; (7) $\alpha\beta\gamma : -$. (When there are alternative ESSs these are given in their probable order of occurrence (see § 2d).) Abbreviations: DB, dominant chick at better position; SB, subordinate chick at better position; B, chick alone at better position; P, chick alone at poorer position.

fitness when sharing the better position than when alone in the poorer position, but the beta offspring still prefers to be alone in the poorer position. Now the only ESS is $\alpha : \beta$, because when the offspring are feeding separately with the alpha sib in the poorer position, it pays this offspring to join the beta offspring in the better position, and the beta offspring then gets a higher fitness by moving to be alone in the poorer position. Because the pay-off to the alpha offspring as dominant sib in the poorer position is lower than being alone in the better position, the alpha offspring does not follow the beta offspring there.

Lastly, there is a region in which both of the sibs have higher fitness sharing the better position than alone in the poorer position, and the ESS is $\alpha\beta : -$. There are parts of this region in which one (the subordinate) or both of the sibs would have higher fitness alone in the better quality position, but neither is assumed to have the ability to expel the other offspring. Thus, even with only two offspring there is a range of possible ESSs. Notably these include the situation in which the alpha sib is in the poorer position when the disparity between the quality of the positions is not too great.

When the family size is three, the offspring must be distributed with two in one position and one at the other, or all three at the same position. For the offspring and parent fitness functions assumed here, the fitness of the alpha and gamma offspring, respectively, is higher as the dominant or subordinate offspring in the better position than as the

dominant or subordinate offspring in the poorer position. Thus, the evolutionarily stable distribution of offspring must occur when there is one offspring alone in the poorer position, because both the alpha and gamma offspring would leave if they found themselves as one of two offspring in the poorer position. It is not clear whether this is the case for all fitness functions. There are then seven regions in terms of the cost of reproduction depending on the quality of the poorer position. When the positions are similar in quality (region 1 in figure 5b), the fitness of an offspring alone at the poorer position is higher than the fitness of the dominant or subordinate sib in the better position, so that all three sibs would have higher fitness if they were the lone offspring in the poorer position. In addition, the fitness of a dominant offspring in the poorer position is higher than of the subordinate offspring in the better position (region 1 in figure 5b), so $\alpha\beta : \gamma$ is not an ESS because when gamma is alone in the poorer position, beta would join it. Gamma would then leave to join alpha because its fitness is higher as the subordinate in the better rather than the poorer position. $\alpha\gamma : \beta$ and $\beta\gamma : \alpha$ are therefore alternative ESSs. Which of them occurs will depend, as for a family size of two, on the additional assumptions made about behavioural interactions

between the sibs. However, in this case, the alpha offspring would have a higher fitness when alone in the poorer position. Thus, the alpha offspring would join a lone beta offspring in the poorer position if this causes the beta to leave, and $\beta\gamma:\alpha$ would be the commoner ESS. In the second region, the fitness of the dominant but not subordinate offspring in the better position is higher than the fitness of a lone offspring in the poorer position. $\beta\gamma:\alpha$ is no longer an ESS because the alpha and gamma offspring agree to swap places. Thus, the ESS is $\alpha\gamma:\beta$. (If such a swap is not allowed the ESS is $\alpha\gamma:\beta$ or $\beta\gamma:\alpha$.) In the third region, being the dominant offspring in the poorer position no longer gives higher fitness than being the subordinate offspring in the better position so $\alpha\beta:\gamma$ becomes an alternative ESS with $\alpha\gamma:\beta$. ($\beta\gamma:\alpha$ is also an ESS if swaps are not allowed.) As argued for the alpha offspring, the beta offspring may be able to impose the ESS that gives it higher fitness because the gamma offspring gains more fitness by moving away from a group of three offspring in the better position. In the fourth region, being the (dominant or) subordinate offspring at the better position gives higher fitness than being the lone offspring in the poorer position, so gamma will no longer swap with alpha. This means that $\alpha\beta:\gamma$, $\alpha\gamma:\beta$ and $\beta\gamma:\alpha$ are all alternative ESSs. Given the fitness gains from moving away from a group of three offspring in the better position, the above sequence is also likely to be the sequence of abundance. Further changes in the ESS occur when an offspring has higher fitness by being one of three sibs in the better position than being alone in the poorer position. Fitness increases with dominance among a group of three sibs sharing a position, so the sequence in which the ESSs with an offspring in the poorer position disappear is $\beta\gamma:\alpha$, then $\alpha\gamma:\beta$, then $\alpha\beta:\gamma$ as the quality of the poorer position decreases, finally leaving $\alpha\beta\gamma:—$ as the ESS. The ESSs in each of the seven regions are listed in the caption to figure 5.

The results show that the interplay between sib competition and the amount of care provided by the parents can lead to a stable distribution of offspring between the two parents. However, it is less clear whether it can explain parentally biased favouritism towards particular kinds of offspring (the model assumes favouritism to individual offspring, and therefore cannot be used to explain it). The 'sib rivalry' hypothesis of Slagsvold (1997a) envisages that a tendency for one parent to feed the more dominant chicks, together with a correlation between some phenotypic character and dominance, leads to an average difference in the type of chick (as specified by the phenotypic character) fed by each parent. However, the model does not predict a strong separation, according to dominance, between the two groups because the beta offspring often attains a higher fitness by being the dominant or lone offspring in the poorer position than by being the subordinate offspring in the better position. This offspring displaces the gamma offspring from the poorer position when both of these are the case. Similarly, in larger families, a separation between the groups according to dominance rank within the entire family would not be stable because it would offer some offspring the opportunity to improve their rank considerably within their feeding group by changing positions. If anything, this would lead to a tendency for each feeding position to be occupied by offspring from alternative dominance ranks within the family.

The above model differs from that of Slagsvold (1997a) in its assumption that offspring cannot divide their time between feeding positions. A model in which this was allowed would require additional assumptions about the consequences of spending different amounts of time at each feeding position relative to the amount of care received. Under some assumptions, the model would tend to collapse to one in which the parents were effectively feeding at the same position.

(e) *Parent-offspring conflict*

The previous model considers a situation in which the two parents feed from different positions, but does not explain why they should do so. Parent-offspring conflict could provide the answer, because the fitness of parents is generally maximized by a more equitable distribution of food than that which maximizes the fitness of individual offspring. Dividing the brood might make it easier for parents to keep track of which offspring have been recently fed (because the group of offspring that they are feeding is smaller; Simmons 1974; Edwards 1985; Harper 1985), or alternatively, because it selects for a more equitable distribution of food (Dean 1980; Slagsvold 1997a).

The second of these ideas can be investigated theoretically by calculating the fitness of the parents if they do, or do not, divide the brood. It will be assumed that the parents have identical fitness functions representing the cost of reproduction, that the offspring are identical and that any division is equal between the two parents, so the parents should agree on whether the family should be split or not. The fitness of each of the parents when they care together is then

$$W_M = NS((c_M + c_F^*)/N) + V - P(c_M) \quad (2.40)$$

and

$$W_F = NS((c_M^* + c_F)/N) + V - P(c_F), \quad (2.41)$$

where N is the family size. The evolutionarily stable amounts of care by each parent can be found by solving the equations $\partial W_M/\partial c_M = 0$ and $\partial W_F/\partial c_F = 0$ where $c_M = c_M^*$ and $c_F = c_F^*$.

$$(\partial W_M/\partial c_M)^* = S'((c_M^* + c_F^*)/N) - P'(c_M^*) = 0 \quad (2.42)$$

and

$$(\partial W_F/\partial c_F)^* = S'((c_M^* + c_F^*)/N) - P'(c_F^*) = 0. \quad (2.43)$$

Eliminating $S'((c_M^* + c_F^*)/N)$ from equations (2.42) and (2.43), $c_M^* = c_F^* = c_{\text{together}}^*$ is the care given by each parent when they care together. Then the fitness of each parent when they care together is

$$W_{P,\text{together}} = NS((2c_{\text{together}}^*)/N) + V - P(c_{\text{together}}^*). \quad (2.44)$$

Conversely, if the parents each provide care separately to half the family,

$$W_M = (N/2)S(2c_M^*/N) + (N/2)S(2c_F^*/N) + V - P(c_M) \quad (2.45)$$

and

$$W_F = (N/2)S(2c_M^*/N) + (N/2)S(2c_F^*/N) + V - P(c_F), \quad (2.46)$$

so that

$$(\partial W_M / \partial c_M)_* = S'(2c_M^*/N) - P'(c_M^*) = 0 \quad (2.47)$$

and

$$(\partial W_F / \partial c_F)_* = S'(2c_F^*/N) - P'(c_F^*) = 0. \quad (2.48)$$

Because the two halves of the family are identical, $c_M^* = c_F^* = c_{\text{apart}}^*$ is the care given by each parent when they care separately. The fitness of each parent when they care apart is

$$W_{P,\text{apart}} = NS((2^*c_{\text{apart}})/N) + V - P(c_{\text{apart}}^*). \quad (2.49)$$

Comparison of equations (2.42), (2.43), (2.47) and (2.48) shows that $c_{\text{together}}^* = c_{\text{apart}}^*$ and substitution into equations (2.44) and (2.49) shows that $W_{P,\text{together}} = W_{P,\text{apart}}$. Thus, when parents control the distribution of care, they have the same fitness whether they care for the offspring together or apart (see table 4d for an illustration).

The same question can be asked for the situation in which offspring control the distribution of care using the model presented in § 2d. Following an argument similar to that for parental control, the fitness of parents when they care separately exceeds that when they care together by $0.062k^{1/3}$ for families of two offspring, and $0.169k^{1/3}$ for families of four offspring (see caption to table 5). Thus, for both of these family sizes the despotic behaviour of dominant offspring results in a distribution of care that selects for the parents to divide the brood and provide care separately to the two halves of the brood. The result for families of four offspring shows that this occurs even when dominant offspring control the distribution of care within each half of the divided brood. Because there is no such selection when parents control the distribution of care, brood division can be regarded as having been selected by parent–offspring conflict. It explains the evolution of parentally biased favouritism for individual offspring and, together with sib competition, might explain parentally biased favouritism for different types of offspring, although the previous section argues that this effect will not be strong.

(f) Sexual conflict

Sexual conflict is an alternative to parent–offspring conflict as a selection pressure for brood division. This occurs when the interests differ of the two parents attending the family. An example is provided in § 2a where, if the brood is divided, there is conflict over which parent cares for which offspring (see table 4a). Such conflict between the parents might lead to selection for pre-emptive departure by one parent, taking the preferred offspring with it.

There are at least three factors that may select for sexual conflict favouring pre-emptive desertion. In the example given in table 4a, both the offspring and parent fitness functions varied. The example given in table 4b shows, however, that a difference in the offspring fitness function alone is sufficient to create sexual conflict over which parent cares for each offspring. In this case, the total fitness accrued through the offspring is the same whichever way the parents care for the two offspring, because the parents have the same cost of reproduction curve and, therefore, would each provide the same amount of care to a given offspring. However, one of the offspring receives more care, so the loss in residual fitness is higher for the parent who cares for it. Both parents would therefore have higher fitness if they cared for the other offspring.

Second, a difference in the cost of reproduction curve between parents (without a difference in the offspring fitness functions) can create sexual conflict, this time over whether brood division should occur at all. If the parents care together for a family of N identical offspring then

$$W_M = NS((c_M + c_F^*)/N) + V_M - P_M(c_M) \quad (2.50)$$

and

$$W_F = NS((c_M^* + c_F)/N) + V_F - P_F(c_F). \quad (2.51)$$

If, however, they each care separately for half the family,

$$W_P = (N/2)S(2c_P/N) + (N/2)S(2c_Q^*/N) + V_P - P_P(c_M). \quad (2.52)$$

Table 4c provides an example where the parental fitness functions differ, but the offspring are identical. When the offspring are cared for separately by the parents, the parent with the steeper cost of reproduction provides more care, and the other parent less care, than when the parents care together. The combined fitness accrued through both offspring is also lower. The parent with the steeper cost of reproduction therefore has higher fitness under biparental care because the benefit through the offspring is higher and the cost to its own residual fitness is lower (because it provides less care). However, the other parent's loss of residual fitness is sufficiently higher under biparental care that it more than compensates for the lower fitness accrued through the offspring, so it has higher fitness overall when the parents each care separately for half the family. There is, thus, conflict over whether the brood should be divided or not (even assuming that the parents each take half) when the cost of reproduction curves differ between the parents. This might select for pre-emptive desertion by the parent who prefers brood division.

Lastly, there may be sexual conflict over the number of offspring that each parent cares for. It was shown in § 2e that when the parents control the distribution of care between identical offspring, and the cost of reproduction curves are the same for both parents, the parents are indifferent as to whether they care for the family together or each care for half the family alone. This is not the case when the parents do not care for equal numbers of offspring. If parent P chooses the number of offspring, n_P , for which it cares (for instance by pre-emptive desertion), then the fitness of each parent is given by

$$W_P = n_P S(c_P/n_P) + (N - n_P)S(c_Q^*/(N - n_P)) + V_P - P(c_P), \quad (2.53)$$

$$W_Q = n_P S(c_P^*/n_P^*) + (N - n_P^*)S(c_Q/(N - n_P^*)) + V_Q - P(c_Q). \quad (2.54)$$

The evolutionarily stable values of the number of young for which it cares, n_P^* , and the care given by each parent, c_P^* and c_Q^* , are given by the equations

$$(\partial W_P / \partial c_P)_* = S'(c_P^*/n_P^*) - P'(c_P^*) = 0, \quad (2.55)$$

$$(\partial W_P / \partial n_P)_* = S(c_P^*/n_P^*) - (c_P^*/n_P^*)S'(c_P^*/n_P^*) - S(c_Q^*/(N - n_P^*)) + (c_Q^*/(N - n_P^*))S'(c_Q^*/(N - n_P^*)) = 0 \quad (2.56)$$

and

$$(\partial W_Q / \partial c_Q)_* = S'(c_Q^*/(N - n_P^*)) - P'(c_Q^*) = 0. \quad (2.57)$$

Figure 6. Sexual conflict over the number of offspring cared for by each of the two parents. The fitness that the parent accrues through the offspring in each part of the brood (broken lines) depends on the number of offspring in that part of the brood. The curves shown here assume that offspring are identical and the costs of care are the same for the two parents, so that these relationships are the same for the offspring in the parent's own care (long dashes) and in the other parent's care (short dashes). However, the cost of care (dashed and dotted line) increases with the number of offspring that the parent cares for itself, so that the parent's overall fitness (solid line), which is the sum of the fitness accrued through offspring in its own care and fitness accrued through offspring in the other parent's care minus the cost of its own care, is maximized when it cares for less than half the brood. Because this maximum is greater than the fitness that the parent would receive when the parents care together for an undivided brood (thin horizontal line), there is sexual conflict in which each parent has maximum fitness when it cares separately for less than half the brood. Fitness values shown here were obtained for divided broods using equations (2.53)–(2.57), and for undivided broods using equations (2.50) and (2.51). The curves shown assume that $S(x) = 0.4(1 - \exp(-1.25(x - 0.4)))$, $P(c) = 0.02c^2$ and $N = 6$.

Figure 6 gives an example for specific offspring and parent fitness functions. As the number of offspring taken by the first parent to leave increases, the fitness that the parent accrues through those offspring ($n_p S(c_p/n_p)$) increases, while the fitness it accrues through the offspring cared for by the other parent ($(N - n_p)S(c_q/(N - n_p))$) decreases in a symmetrical fashion. However, the cost to the first parent to leave, $P(c_p)$, increases with the number of offspring that it takes with it, so that its total fitness, which is the sum of these three components, peaks when it takes less than half the family. The fitness at this point is higher than the fitness that it would receive if both parents cared together for the whole family, so pre-emptive desertion is selected for. The other parent's fitness is lower under pre-emptive desertion by its mate than under biparental care of the whole family, but it is assumed to be unable to do anything to prevent it.

These models explain brood division (parentally biased favouritism for different individual offspring) by the assumption that pre-emptive desertion enables one parent to win when there is sexual conflict. Single-shot sealed bid models are appropriate to a decision concerning pre-emptive desertion, but not if brood division was not permanent, as is the case for nestlings or if chicks can be exchanged between parents after the initial division (Smith 1978; Smith & Merkt 1980; Harper 1985). It would be particularly interesting to know whether models of evolutionarily stable negotiation rules (McNamara *et al.* 1999) ever predict that parents can win in sexual conflict by caring for a restricted subset of a physically undivided brood of nestlings.

The factors considered above differ in their ability to explain parentally biased favouritism with respect to offspring type. Conflict over the number of young to be cared

for should select equally for pre-emptive desertion by each parent. Even if one parent has greater opportunities for pre-emptive desertion, and therefore does so more often, all offspring are assumed to offer the same benefits, so the deserting parent should not prefer particular offspring. Conflict over which offspring each parent cares for explains why the deserting parent should take a particular kind of offspring, but not why one parent should desert more often, because the benefits of pre-emptive desertion are the same for both parents. A difference between the parents in the opportunity to pre-emptively desert would generate parentally biased favouritism in relation to offspring type. Lastly, sexual conflict created by a difference in the cost of reproduction curves has the opposite effect to a difference in the benefits of care: only one parent is selected to desert, but there is no reason for this parent to take particular types of offspring with it. However, if these two factors are combined, one parent is more strongly selected to take the preferred offspring (see table 4a), and this might lead to that parent pre-emptively deserting more often. Differences in the offspring and parent fitness curves might therefore together select for parentally biased favouritism for different types of offspring.

3. DISCUSSION

Table 6 provides a summary of the main conclusions of the models. Two main patterns emerge: first, parentally biased favouritism towards different kinds of offspring in undivided broods can be explained when there are differences between the parents in the benefits or costs of care given to different types of offspring; but the bias is extreme, with at least one parent caring for only one type of offspring. Second, evolutionary conflict, whether

Table 6. A summary of the predictions of the models.

offspring and parental fitness functions, and control of division of care among offspring (if not by parents) hypothesis	assumption over brood division	explains parental favouritism to different	
		individual offspring (= brood division) ^a	types of offspring
(a) offspring differ in benefits of care, parents differ in costs of care	undivided	—	no
(b) as in (a)	divided	—	sexual conflict (see below)
(c) as in (a), but parents differ in benefits of care from given types of offspring	undivided	—	yes, but extreme
(d) as in (a), but parents differ in effort incurred in caring for given	undivided	—	yes, but extreme
<i>sib competition and parent-offspring conflict</i> (e) offspring identical in benefits, parents identical in costs offspring despotically control division of care	divided	—	unlikely
(f) as in (e) but parents decide whether to divide brood	—	yes	unlikely
<i>sexual conflict</i> (g) offspring identical in benefits, parents identical in costs brood divided equally if divided	—	no	no
(h) as in (g), but parents may divide brood unequally	—	yes	no
(i) as in (g), but offspring differ in benefits	—	yes	yes, if parents differ in opportunity for desertion
(j) as in (g), but parents differ in costs	—	yes	no
(k) as in (g), but offspring differ in benefits, and parents differ in costs	—	yes	yes, if parents differ in opportunity for desertion or relative strength of selection determines which parent deserts

^a The model makes an assumption about whether the brood is divided or not; it cannot make a prediction about brood division.

between parents and offspring or between the two parents, is a major selection pressure for brood division.

One way of conceptualizing the results for undivided broods is as a series of transactions in which residual fitness is successively converted into effort, care and offspring fitness (figure 7). The relationships defining the rates of conversion may differ between the two parents. For instance, the parents may differ in their cost of reproduction curves, which define the conversion rate of residual fitness into effort. In addition, the parents may have choices as to the pathway they use to carry out a particular conversion. For instance, care may be converted into offspring fitness via offspring of different types. However, parentally biased favouritism only occurs when there is a difference between the parents in the relationships governing the rates of conversion after a decision point as

to the pathway used (i.e. broken arrows (indicating different relationships in the two parents) occur after a branching point in figure 7). For instance, when the costs of care differ between the parents and the benefits of care differ between the offspring (figure 7a), the two parents convert residual fitness into care at different rates. However, the relationships that govern the conversion of care into offspring fitness are the same for the two parents, so when the two types of offspring offer equally good conversion rates (strictly speaking marginal conversion rates) for one parent, they also do so for the other parent. Because both parents are then indifferent as to the amount they use each conversion route, the model makes no prediction as to parentally biased favouritism in respect of offspring type. If, however, the parents differ in the benefits of care from different types of offspring (figure 7b), the conversion rates

Figure 7. A conceptual model of parental care. Parental care is seen as a series of transactions, represented by arrows, in which the residual fitness of the parent is converted successively into effort, care and offspring fitness. The relationships defining the conversion rates may be the same for the two parents (solid arrows) or differ between the two parents (broken arrows). Branched arrows indicate alternative conversion pathways. Consistent differences between the two parents in the amount that alternative pathways are used are predicted only when sex differences in the relationships governing conversion rates occur after a branch in the pathways (see § 3).

of care into offspring fitness must differ between the parents for at least one of the offspring types. (This excludes the case where the offspring fitness functions for one parent are a constant multiple of those for the other parent across all offspring types; see equation (2.18).) This, in turn, means that the conversion rates for the two offspring types can only be the same for, at most, one of the parents. For the other parent, one of the offspring types offers a superior conversion rate and it cares only for that offspring type, bringing about parentally biased favouritism. In general, when there are more than two offspring types, the parents will both care for, at most, one of the offspring types. The situation in which the parents differ in the cost of care given to different types of offspring can be envisaged as one in which there are two types of care, distinguished by the offspring type for which the care is destined (figure 7c). Again, a difference between the parents in the relationships defining the conversion rates occurs after the decision point, and one parent uses only one of the pathways, resulting in parentally biased favouritism.

This conceptualization of parental investment offers some insights into the consequences of multi-dimensional care (figure 7d). All of the models described assume that care is unidimensional. When there is more than one type of depreciable care (for instance, food contains more than one type of nutrient), the fitness of an offspring will be a function of the amounts of each of these types of care that it receives. As before, the functions will vary between offspring types. Focusing first on the conversion of each type of care into offspring fitness, there is no reason to suppose that these relationships differ between the parents (except for the reasons given in § 2c above). If this is the case, then for each type of care the total amount given to each type of offspring is adjusted so that the marginal conversion rates are equal, but then the two parents will be indifferent as to how much they use each pathway. Thus, parentally biased favouritism is not predicted within any given type of care. However, given the assumptions shown in figure 7d, parents are not indifferent to the type of care they give. It is assumed that each kind of care requires fixed amounts of different kinds of effort (time and energy

for instance) that do not differ between the parents. However, because of differences in the biology of the two sexes, the two parents differ in the costs, in terms of residual fitness, of making different kinds of effort. These assumptions add up to a situation in which the relationships defining the conversion rate of residual fitness into care of each type differ between the two parents after a decision point, and at least one parent is expected to use only one of the pathways and make only one type of care. Thus, under these assumptions, parentally biased favouritism in terms of the type of care, but not in terms of the amount of a given type of care, is expected. This supports and clarifies the argument given in § 1. Moreover, by applying the previous logic, one type of care, at most, is expected from both parents. Given that the assumptions made in figure 7d probably represent an extremely widespread situation in species with sexual dimorphism, the question then becomes: why, in species with biparental care, is there usually more than one type of care (e.g. provisioning and predator defence) provided by both parents. The answer is probably that the above prediction only applies when both forms of care are depreciable and the effort expended on making one type of care cannot be simultaneously used in making another (as would be the case when parents can search for two different types of food simultaneously). The tendency in traditional human societies for each parent to provide different parts of an offspring's diet (Kaplan *et al.* 2000) might be one example.

The results obtained for parentally biased favouritism towards different types of offspring, when the brood is undivided, suggest that when it does occur it should be extreme, with all but, at most, one of the offspring types being cared for by only one parent. However, all the examples given in tables 1 and 2 are more moderate in the degree of bias. The most probable explanation is that discriminating between offspring incurs a cost. However, whether a cost of discrimination leads to less than extreme parentally biased favouritism depends on how the costs of discrimination act. For instance, under the assumptions of the basic model (parents differ in the cost of care and offspring in the benefits of care, but parents do not differ in the benefit they receive from any given offspring type), if the effort made in discrimination is additive with that made in care giving and does not differ between the parents, there are evolutionarily stable levels of discrimination and care giving but the model does not predict the proportions of each implemented by each of the two parents. (This is because the model is exactly analogous to the basic model except that the choice for the parents is in providing care discriminately or indiscriminately, rather than caring for different types of chicks. The model therefore makes analogous predictions.) If, however, the situation is analogous to the model in which the effort incurred in caring for different types of offspring differs between the parents, so that the effort involved in discriminating differs between the parents, one or both parents is expected to provide either only discriminate or only indiscriminate care. (In other words, the model never predicts that both parents provide both discriminate and indiscriminate care.) Although this prediction is extreme in terms of the choice made by the parents it may lead to intermediate bias in the care provided (for instance, when both parents provide indiscriminate care and one parent

also provides discriminate care). This situation recalls that found in eastern bluebirds (*Sialia sialis*), in which female parents feed sons and daughters approximately equally, whereas males preferentially feed daughters (Gowaty & Droge 1991). This would not require any difference between the parents in the benefits of caring for given types of offspring (i.e. parentally biased favouritism would not be predicted in this situation without a cost of discrimination). Lastly, the parents may differ in the benefit they receive from different types of offspring, so that extreme bias is favoured when discrimination is costless, but the costs of discrimination may be such that a less than perfect discrimination mechanism gives the parents their highest fitness.

The second major pattern that emerges from the models is that brood division is an apparently universally predicted outcome of evolutionary conflicts of interest, whether between parents and offspring or between the two parents. However, the parents of many species care together for an undivided brood. One explanation for this is that not all forms of parental care are depreciable (Lazarus & Inglis 1986). For instance, a major part of the effort of nest building would need to be repeated if the brood was divided completely during the nestling phase. A second explanation is that offspring fitness depends on family size *per se*. For instance, nestlings gain thermoregulatory benefits from being in a larger brood (Mertens 1969). Conversely, benefits that vary negatively with family size *per se* will select for brood division. This includes several of the hypotheses for brood division listed by McLaughlin & Montgomerie (1985), including minimizing predation and increasing foraging efficiency.

The previous discussion reveals a number of simplifying assumptions. Nevertheless, the models presented offer several important insights. (i) They show that some previous models, notably those associated with the idea that only the parent who receives the higher benefit or has the lower costs can afford to invest in offspring of low value, are untenable in their stated form. (ii) The models suggest that if parentally biased favouritism with respect to offspring type occurs it should be extreme, and that selection pressures favouring brood division and parental bias in the kind of care provided commonly occur. Viewed from that perspective, the problem becomes not how to explain parentally biased favouritism, but rather how to explain why it is not more intense and widespread.

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